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Moisture activation and carbon use efficiency of soil microbial communities along an aridity gradient in the Atacama Desert

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ABSTRACT

Due to their extreme aridity, high rate of UV irradiation and low soil carbon (C) content, the soils of the Atacama Desert represent one of the world's most hostile environments for microbial life and its survival. Although infrequent, climatic conditions may, however, prevail which temporarily remove these stresses and allow life to briefly flourish. In this study we investigated the response of soil microbial communities to water and C availability across an aridity gradient (semi-arid, arid, hyper-arid) within the Atacama Desert. We simulated the impact of hyper-dry spells, humid fogs and precipitation events on the activation of the microbial community and the subsequent mineralization of low (glucose) and high (plant residues) molecular weight C substrates. Our results showed that mineralization rate followed the trend: semi-arid > arid > hyper-arid. Some glucose mineralization was apparent under hyper-arid conditions (water activity, a_w = 0.05), although this was 10-fold slower than under humid conditions and ca. 200-fold slower than under wet conditions. A lag phase in CO_2 production after glucose-C addition in the hyper-arid soils suggested that mineralization was limited by the low microbial biomass in these soils. No lag phase was apparent in the corresponding semi-arid or arid soils. In contrast, the breakdown of the plant residues was initially much slower than for glucose and involved a much longer lag phase in all soils, suggesting that mineralization was limited by low exoenzyme activity, particularly in the humid and hyper-dry soils. Our results also showed that microbial C use efficiency followed the trend: hyper-arid > arid > semi-arid. In conclusion, we have shown that even under hyper-arid conditions, very low levels of microbial activity and C turnover do occur. Further, the microbial communities are capable of rapidly responding to available C once water becomes more abundant, however, this response is both biomass and metabolically limited in hyper-arid soils.

Keywords: Carbon cycling; Climate extreme; Desert Microbiology; Moisture availability; Xeric; Yungay

The hyper-arid soils of the Atacama experience some of the most severe climatic conditions on Earth, and are often used to understand the potential for life on exoplanets such as Mars (Valdivia-Silva et al., 2012; McKay, 2014). These soils contain very low organic carbon (OC) concentrations, with labile OC values varying from 2-73 µg C g^{-1} (Valdivia-Silva et al., 2012; Fletcher et al., 2012). The role of (hyper)arid conditions on soil OC processing vs. stabilization continues to be debated (e.g. Skelley et al., 2007; Ewing et al., 2006; 2008; Ziolkowski et al., 2013; Wilhelm et al., 2017).

Microbial soil communities in the hyper-arid core of the Atacama Desert are of low abundance and express numerous xero-tolerance traits (Azua-Bustos et al., 2015; Connon et al., 2007; Drees et al., 2006; Lebre et al., 2017; Navarro-Gonzalez et al., 2003). Their activity is primarily limited by water, although other factors such as C limitation, high salinity and UV irradiation may also impose constraints on life (Warren-Rhodes et al., 2006; Gomez-Silva et al., 2008). Although extremely infrequent, the microbial biomass can be subject to precipitation events (Jordan et al., 2015) or more likely to high humidity and fog-derived water (Cáceres et al., 2007). In this context, our aims were to (1) determine the reactivation speed of the soil microbial community to moisture and OC addition, (2) compare the relative mineralization rate of low and high molecular weight OC substrates in soil, and (3) investigate the C use efficiency (CUE) of these communities.

The Atacama is a temperate desert and extends from ca. 15 to 35°S and between 70 to 72°W along South America's Pacific Coast. Hyperarid conditions have existed in the Atacama desert for ca. 25 Ma (Dunai et al., 2005). The mean annual rainfall in the hyperarid core is <1

69 mm y^{-1}; a single rainfall event of 1-20 mm may occur once in a decade (Warren-Rhodes et al.,
70 2006, McKay et al., 2003).

71 Field sampling was undertaken in the Atacama region of Chile in February, 2014. Soil
72 samples were taken from the surface soil (0-10 cm; n = 3) and subsoil (20-40, 120-140 cm; n
73 = 1) were collected from the hyper-arid site at Yungay (1020 m a.s.l.; 24°8'54.67"S;
74 70°7'32.48"W). Yungay is probably the most frequently studied hyper-arid region of the
75 Atacama Desert, having an extremely low water availability (Navarro-Gonzalez et al., 2003;
76 Azua-Bustos et al., 2015). Surface samples (0-10 cm, n = 3 at 5 sites) were also taken in the
77 Andean Precordillera at Quebrada Aroma (19°31'42.7"S; 69°22'43.2"W to 19°46'53.1"S;
78 69°40'02.4"W). This precipitation gradient transect was characterized by decreasing vegetation
79 cover and plant diversity from arid (2020-2720 m a.s.l.; 3 sites) to hyper-arid sampling sites
80 (1340-1660 m a.s.l.; 2 sites). Finally, additional surface (0-10 cm, n = 3) and subsurface soils
81 (n = 1) were sampled down to 2 m near Paposo in the semi-arid Coastal Cordillera (570 m
82 a.s.l.; 25°00'43.02"S; 70°26'47.50"W). The samples from all sites had a low intrinsic moisture
83 content at the time of collection (20.4 ± 4.1 g kg^{-1}). All samples were homogenised by sieving
84 (<2 mm) and stored in sealed tubes prior to use. Based on their moisture regime, the sites were
85 divided into 3 levels of aridity, namely, semi-arid, arid and hyper-arid (see Supplementary
86 information for further details and basic chemical data).

87 The experiments used two contrasting forms of C to determine how microbial activity
88 was regulated by substrate quality: (1) low molecular weight (MW) substrate (^{14}C-labelled
89 glucose); (2) high MW substrate (^{14}C-labelled dry *Lolium perenne* L. shoots; Hill et al., 2007;
90 Simfukwe et al., 2011). In addition, to explore their response to moisture availability we used
91 three moisture regimes: (1) *wet*, in which water was added directly to the soil surface to
92 simulate desert rainfall, (2) *humid*, in which the soil samples were maintained at a high relative
93 humidity to simulate desert fogs, and (3) *hyper-dry*, in which the soil samples were incubated

at a low relative humidity to simulate typical conditions in the hyper-arid region of the Atacama Desert.

For each sample, 1 g of field soil was placed into sterile 50 cm^3 polypropylene containers. Either ^{14}C-labelled glucose (72 mg C kg^{-1} soil; 0.44 MBq kg^{-1} soil) or 100 mg of ^{14}C-plant material (100 g kg^{-1} soil; 42 g C kg^{-1} soil; 3.6 MBq kg^{-1} soil) was then added to the soil. For the *humid* treatments, the ^{14}C-glucose was first dried down under N_2 onto a sterile quartz sand carrier before addition to the soil (100 g sand kg^{-1} soil), while the dried ^{14}C-labelled plant material was added directly to the soil. The relative humidity in the *humid* (simulated fog) containers was 67±3% at the start and was 83±3% at the end. For the *wet* treatments (simulated rainfall), the ^{14}C substrates were added as described above, but together with 100 µl of distilled water. For the *hyper-dry* treatments (simulated normal conditions), the method was identical to the *humid* treatment, except that the containers also contained a small vial of desiccant (1 cm^3; Drierite®; Sigma-Aldrich, Poole, UK) to maintain a relative humidity of 1-5% (Reis et al., 2009). In the *wet* and *humid* treatments, $^{14}CO_2$ evolved from the soil was captured with a vial of 1 M NaOH trap placed inside the container (Glanville et al., 2016), while in the *hyper-dry* treatment it was trapped with a vial containing 40 mg of solid $Ba(OH)_2.8H_2O$. After addition of the ^{14}C-substrates and $^{14}CO_2$ traps, the containers were hermetically sealed and incubated at 20°C. The $^{14}CO_2$ traps were replaced daily for 14 d. The length of experiment reflects the typical time that water may remain in soil after a rare precipitation event (McKay et al., 2003). The $^{14}CO_2$ in the traps was determined by liquid scintillation counting using Optiphase 3 scintillation fluid (PerkinElmer Corp., Waltham, MA) and a Wallac 1404 Liquid Scintillation Counter (PerkinElmer Corp.). To determine how much ^{14}C-glucose remained in the soil at the end of the incubation, the soils were extracted with 10 ml of 0.5 M NaCl (200 rev min^{-1}; 10 min), centrifuged (18,000 *g*; 15 min) and the ^{14}C content of the extract determined as described above.

To account for $^{14}CO_2$ produced by the intrinsic microbial community present in the ^{14}C-labelled plant material (e.g. phyllosphere community), control incubations were also performed in the absence of soil.

Substrate C use efficiency was calculated according to Glanville et al. (2016) (see Supplementary on-line information). All statistical analyses (repeated measures ANOVA, linear regression, paired t-tests) were performed in Minitab v16.2 (Minitab Inc., State College, PA) using $P < 0.05$ as the level for statistical significance.

The effect of soil aridity status and substrate quality on the rate of C mineralization is shown in Figure 1. Overall, mineralization followed the series: *semi-arid* > *arid* > *hyper-arid* for the different soils ($P < 0.001$), and *wet* > *humid* > *hyper-dry*, for the three moisture regimes ($P < 0.001$; Fig. S8). There was an immediate microbial response to the application of glucose for all soils and under all three moisture treatments (Fig. 1a), however, the rate was 180-times slower in the *hyper-dry* treatments compared to the *wet* treatment (Table S9). In contrast to glucose, a significant lag phase in mineralization was seen in the soils amended with ^{14}C-plant residues. This lasted for 1-5 d in the *wet* treatment and 6-8 d in the *humid* treatment. Although some mineralization was apparent in the *hyper-dry* treatment, the rates of $^{14}CO_2$ evolution remained low and relatively constant throughout the 14 d incubation period (<0.3% for glucose and <0.1% for plant material). Some mineralization of the plant material was apparent when soil was not present; however, this was only of significance in the *wet* treatment (dotted lines in Fig. 1).

A strong positive correlation was apparent between the initial mineralization rate of low (glucose) and high molecular weight C (plant residues) across all soils for the *wet* and *humid* treatments ($r^2 = 0.71$, Fig. S5). Overall, the rate of mineralization of glucose was 14.7 ± 3.6 times faster than the plant material under *wet* conditions and was 14.0 ± 2.9 times faster under *humid* conditions ($P = 0.864$).

144 Extractions of the soil at the end of the experiments showed a negative correlation
145 between the amount of $^{14}CO_2$ produced and ^{14}C-glucose depletion from the soil (r^2 = 0.81; Fig.
146 S4), and with almost all the ^{14}C-glucose being removed from some of the *wet* soils after 14 d.
147 Not all of the ^{14}C-glucose was mineralized, however, with $^{14}CO_2$ production reaching a plateau
148 in the *wet* glucose treatment at ca. 45% for the semi-arid soils and ca. 25% for the arid soils.
149 As very little ^{14}C-glucose remained in solution at the end of the experiment, particularly in the
150 semi-arid soils, we assumed that the remainder of the ^{14}C had been immobilized in the
151 microbial biomass (see Section S4; Fig. S4). From this, we estimated microbial C use efficiency
152 (CUE) in the *wet* glucose treatment. Across all samples, CUE showed a strong negative
153 correlation with mineralization rate and followed the trend: hyper-arid > arid > semi-arid (0.77
154 ± 0.03, 0.53 ± 0.04 and 0.46 ± 0.03, respectively; Fig. 2).
155 In order of importance, our results show that soil microbial activity in the Atacama Desert
156 is constrained by: (i) available soil moisture, (ii) intrinsic microbial biomass, and (iii) the type
157 of organic C substrate. In addition, soil depth is also a major limiting factor (see Supplementary
158 Information). The typical limit for soil microbial activity occurs at a_w values of ca. 0.6 (-70
159 MPa), well below the point at which plant life ceases (-1.5 MPa; Grant, 2004; Roberts and
160 Ellis, 1989; de Goffau, et al., 2011). At an a_w of 0.6, the water films in our soils can be expected
161 to be only a few water monolayers thick (3-10 nm; Leao and Tuller, 2014; Ruis et al., 2016).
162 Consequently, the catalytic activity and mobility of exoenzymes (ca. 3-50 nm diameter) will
163 be minimal below this a_w point (Sirotkin, 2005), while microbial movement will be impossible
164 even for nano-sized archaea and bacteria (<600 nm diameter; Stark and Firestone, 1995). The
165 hyper-arid region of the Atacama Desert remains below the critical a_w value of 0.6 for ca. 90%
166 of the year, at which point no microbial activity is expected to occur (Wierzchos et al., 2011).
167 Although extremely small, some C substrate mineralization, however, was observed in all soils
168 under *hyper-dry* conditions (a_w = 0.05; -410 MPa). This is most likely attributable to abiotic

mineral-driven oxidation of organic C (Quinn et al., 2005), or possibly in some of our soils due to isolated pockets of microbial activity protected within hyper-saline or nanoporous structures (Robinson et al., 2015; Wierzchos et al., 2015; Lebre et al., 2017). Under these *hyper-dry* conditions, however, the diffusion of substrates will severely restrict microbial uptake of exogenous C (diameter of glucose = 0.8 nm). Under the *humid* soil moisture regime, much greater microbial activity was observed. The lag phase in glucose-use under these conditions was consistent with the dynamics of water sorption to the soil, which permitted microbial activity to commence, although any microbial movement will still be restricted (Fig. S9; de Goffau et al., 2011). This lag phase could also be attributable to microbial growth; however, the lack of a classic sigmoidal response in the hyper-arid soil does not favor this explanation. In comparison to the glucose treatment, the longer lag phase in the *humid* plant residue treatment suggests that C mineralization was limited by both a lack of water and exoenzymes. In addition, it may also reflect the slow rate of diffusion of low MW solutes released from the plant residues to the microbial community. In addition, the greater rate of breakdown of plant residues in comparison to glucose in the hyper-dry soil suggests that the soil microbial community is metabolically constrained (i.e. due to a lack of enzymes to assimilate glucose or a lack of other organic or inorganic solutes). As the C-to-N ratio of the soil and the levels of available N, P and other nutrients are relatively high in these soils (Table S1), substrate overload is a more likely explanation. This lack of capacity to assimilate the added glucose-C is also supported by the lack of sustained microbial growth when supplied with high rates of this C substrate, even under *wet* conditions, and the very high C use efficiency within the microbial community. Our evidence suggests that while glucose-C can be transported into the cell, it cannot be readily used in respiration. Potentially, this C is being allocated to internal storage pools or to other C-rich structures (Russell, 2007; de Goffau, et al., 2008; Lebre et al., 2017). Further work on the metabolic and transcriptomic profiling of these microbial

communities is clearly needed to help address this issue. In summary, our results provide evidence of slow rates of C turnover under hyper-dry conditions. When humid fogs occur, we show that the microbial communities are capable of responding relatively quickly, particularly in soils which favor better long-term microbial survival (i.e. semi-arid rather than hyper-arid). When free water is present, the constraints on C use are largely removed and high rates of microbial activity commence immediately, mirroring the response in other non-arid soils (Jones and Murphy, 2007).

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References

Azua-Bustos, A., Urrejola, C., Vicuña, R., 2012. Life at the dry edge: Microorganisms of the Atacama Desert. FEBS Letters 586, 2939-2945.

Azua-Bustos, A., Caro-Lara, L., Vicuña, R., 2015. Discovery and microbial content of the driest site of the hyperarid Atacama Desert, Chile. Environmental Microbiology Reports 7, 388-394.

Cáceres, L., Gómez-Silva B., Garró, X., Rodríguez, V., Monardes, V., McKay, C.P., 2007. Relative humidity patterns and fog water precipitation in the Atacama Desert and biological implications. Journal of Geophysical Research Biogeosciences 112, G04S14.

Cockell, C.S., Mckay, C.P., Warren-Rhodes, K., Horneck, G., 2008. Ultraviolet radiation-induced limitation to epilithic microbial growth in and deserts - Dosimetric experiments in the hyperarid core of the Atacama Desert. Journal of Photochemistry and Photobiology B-Biology 90, 79-87.

219 Connon, S.A., Lester, E.D., Shafaat, H.S., Obenhuber, D.C., Ponce, A., 2007. Bacterial
220 diversity in hyperarid Atacama Desert soils. Journal of Geophysical Research
221 Biogeosciences 112, G04S17.
222 de Goffau, M.C., Yang, X.M., van Dijl, J.M., Harmsen, H.J.M., 2009. Bacterial pleomorphism
223 and competition in a relative humidity gradient. Environmental Microbiology 11, 809-822.
224 de Goffau, M.C., van Dijl, J.M., Harmsen, H.J.M., 2011.Microbial growth on the edge of
225 desiccation. Environmental Microbiology 13, 2328-2335.
226 Drees, K.P., Neilson, J.W., Betancourt, J.L., Quade, J., Henderson, D.A., Pryor, B.M., Maier,
227 R.M., 2006. Bacterial community structure in the hyperarid core of the Atacama Desert,
228 Chile. Applied and Environmental Microbiology 72, 7902-7908.
229 Dunai, T.J., González-López, G.A., Juez-Larré, J., 2005. Oligocene-Miocene age of aridity in
230 the Atacama Desert revealed by exposure dating of erosion-sensitive landforms. Geology
231 33, 321-324.
232 Evenstar, L.A., Hartley, A.J., Stuart, F.M., Mather, A.E., Rice, C.M., Chong, G., 2009.
233 Multiphase development of the Atacama Planation Surface recorded by cosmogenic 3He
234 exposure ages, implications for uplift and Cenozoic climate change in western South
235 America. Geology 37, 27-30.
236 Ewing, S., Sutter, B., Amundson, R., Owen, J., Nishiizumi, K., Sharp, W., Cliff, S., Perry, K.,
237 Dietrich, W., McKay, C., 2006. A threshold in soil formation at Earth's arid-hyperarid
238 transition. Geochimica Cosmochimica Acta 70, 5293-5322.
239 Ewing, S., Macalady, J., Warren-Rhodes, K., McKay, C., Amundson, R., 2008. Changes in the
240 soil C cycle at the arid-hyperarid transition in the Atacama Desert. Journal of Geophysical
241 Research Biogeosciences 113, G02S90.
242 Fletcher, L.E., Conley, C.A., Valdivia-Silva, J.E., Perez-Montaño, S., Condori-Apaza, R.,
243 Kovacs, G.T., Glavin, D.P., McKay, C.P., 2011. Determination of low bacterial

concentrations in hyperarid Atacama soils: Comparison of biochemical and microscopy methods with real-time quantitative PCR. Canadian Journal of Microbiology 57, 953-963.

Fletcher, L.E., Valdivia-Silva, J.E., Perez-Montano, S., Condori-Apaza, R., Conley, C.A., McKay, C., 2012. Variability of organic material in surface horizons of the hyper-arid Mars-like soils of the Atacama Desert. Advances in Space Science 49, 271-279.

Glanville, H., Hill, P.W., Schnepf, A., Oburger, E., Jones, D.L., 2016. Combined use of empirical data and mathematical modelling to better estimate the microbial turnover of isotopically labelled carbon substrates in soil. Soil Biology & Biochemistry 94, 154-168.

Garreaud, R., Barichivich, J., Christie, D.A., Maldonado, A., 2008. Interannual variability of the coastal fog at Fray Jorge relict forests in semiarid Chile. Journal of Geophysical Research Biogeosciences 113, G04011.

Gómez-Silva, B., Rainey, F.A., Kimberley, F.A., Warren-Rhodes, A., McKay, C.P., Rafael Navarro-González, R., 2008. Atacama Desert Soil Microbiology. In: Microbiology of Extreme Soils. pp 117-132. Eds. Dion, P., Nautiyal, C.S., Soil Biology Volume 13. Springer Verlag, Berlin.

Jones, D.L., Murphy, D.V., Microbial response time to sugar and amino acid additions to soil. Soil Biology & Biochemistry 39, 2178-2182.

Jordan, T.E., Riquelme, R., González, G., Herrera, C., Godfrey, L., Colucci, S., Gironás León, J., Gamboa, C., Urrutia, J., Tapia, L., Centella, K., Ramos, H., 2015. Hydrological and geological consequences of the extreme precipitation event of 24-26 March 2015. In: Conference Proceedings, XIV Congreso Geológico Chileno, La Serena. Sociedad Geológica de Chile.

Hill, P.W., Marshall, C., Williams, G.G., Blum, H., Harmens, H., Jones, D.L., Farrar, J.F., 2007. The fate of photosynthetically-fixed carbon in *Lolium perenne* L. grassland as

modified by elevated CO_2, nitrogen and sward management. New Phytologist 173, 766-777.

Houston, J., Hartley, A.J., 2003. The central Andean west-slope rainshadow and its potential contribution to the origin of hyper-aridity in the Atacama Desert. International Journal of Climatology 23, 1453-1464.

Leao, T.P., Tuller, M., 2015. Relating soil specific surface area, water film thickness, and water vapor adsorption. Water Resources Research 50, 7873-7885.

Lebre, P.H., De Maayer, P., Cowan, D.A., 2017. Xerotolerant bacteria: surviving through a dry spell. Nature Reviews Microbiology 15, 285-296.

Lester, E.D., Satomi, M., Ponce, A., 2007. Microflora of extreme arid Atacama Desert soils. Soil Biology & Biochemistry 39, 704-708.

McKay, C.P., Fridmann, I., Gómez-Silva, B., Cáceres-Villanueva, L., Anderson, D.T., Landheim, R., 2003. Temperature and moisture conditions for life in the extreme arid region of the Atacama Desert: four years of observation including El Nino of 1997-1998. Astrobiology 3, 393-406.

McKay, C.P., 2014. Requirements and limits for life in the context of exoplanets. Proceedings of the National Acadamy of Sciences USA 111, 12628-12633.

Navarro-González, R., Rainey, F.A., Molina, P., Bagaley, D.R., Hollen, B.J., de la Rosa, J., Small, A.M., Quinn, R.C., Grunthaner, F.J., Cáceres, L., Gomez-Silva, B., McKay, C.P., 2003. Mars-like soils in the Atacama Desert, Chile, and the dry limit of microbial life. Science 302, 1018-1021.

Neilson, J.W., Quade, J., Ortiz, M., Nelson, W.M., Legatzki, A., Tian, F., LaComb, M., Betancourt, J.L., Wing, R.A., Soderlund, C.A., Maier, R.M., 2012. Life at the hyperarid margin: novel bacterial diversity in arid soils of the Atacama Desert, Chile. Extremophiles 16, 553-566.

293 Paulino-Lima, I.G., Azua-Bustos, A., Vicuña, R., Gonzalez-Silva, C., Salas, L., Teixeira, L.,
294 Rosado, A., Leitao, A.A.D., Lage, C., 2013. Isolation of UVC-tolerant bacteria from the
295 hyperarid Atacama Desert, Chile. Microbial Ecology 65, 325-335.
296 Quade, J., Rech, J.A., Latorre, C., Betancourt, J.L., Gleeson, E., Kalin, M.T.K., 2007. Soils at
297 the hyperarid margin: the isotopic composition of soil carbonate from the Atacama Desert,
298 Northern Chile. Geochimica Cosmochimica Acta 71, 3772-3795.
299 Quinn, R.C., Zent, A.P., Grunthaner, F.J., Ehrenfreund, P., Taylor, C.L., Garry, J.R.C., 2005.
300 Detection and characterization of oxidizing acids in the Atacama Desert using the Mars
301 Oxidation Instrument. Planetary and Space Science 53, 1376-1388.
302 Roberts, E.H., Ellis, R.H., 1989. Water and seed survival. Annals of Botany 63, 39-52.
303 Robinson, C.K., Wierzchos, J., Black, C., Crits-Christoph, A., Ma, B., Ravel, J., Ascaso, C.,
304 Artieda, O., Valea, S., Roldán, M., Gómez-Silva, B. and DiRuggiero, J., 2015. Microbial
305 diversity and the presence of algae in halite endolithic communities are correlated to
306 atmospheric moisture in the hyper-arid zone of the Atacama Desert. Environmental
307 Microbiology 17, 299-315.
308 Ruiz, H.A., Sarli, G.O., Schaefer, C.E.G.R., Filgueira, R.R., de Souza, F.S., 2016. Specific
309 surface of oxisols and its relationship with water retention. Revista de la Facultad de
310 Ciencias Agrarias 48, 95-105.
311 Russell, J.B., 2007. The energy spilling reactions of bacteria and other organisms. Journal of
312 Molecular Microbiology and Biotechnology 13, 1-11.
313 Simfukwe, P., Hill, P.W., Emmett, B.A., Jones, D.L., 2011. Soil classification provides a poor
314 indicator of carbon turnover rates in soil. Soil biology & Biochemistry 43, 1688-1696.
315 Sirotkin, V.A., 2005. Adsorption of vapors of water and dioxane on bovine pancreas alpha-
316 chymotripsin. Russian Journal of Physical Chemistry 79, 2034-2039.

317 Skelley, A.M., Aubrey, A.D., Willis, P.A., Amashukeli, X., Ehrenfreund, P., Bada, J.L.,
318 Grunthaner, F.J., Mathies, R.A., 2007. Organic amine biomarker detection in the Yungay
319 region of the Atacama Desert with the Urey instrument, Journal of Geophysical Research
320 Biogeosciences 112, G04S11.
321 Stark, J.M., Firestone, M.K., 1995. Mechanisms for soil-moisture effects on activity of
322 nitrifying bacteria. Applied and Environmental Microbiology 61, 218-221.
323 Valdivia-Silva, J.E., Navarro-Gonzalez, R., Fletcher, L., Perez-Montano, S., Condori-Apaza,
324 R., McKay, C.P. 2012. Soil carbon distribution and site characteristics in hyper-arid soils
325 of the Atacama Desert: a site with Mars-like soils.
326 Warren-Rhodes, K.A., Rhodes, K.L., Pointing, S.B., Ewing, S.A., Lacap, D.C., Gómez-Silva,
327 B., Amundson, R., Friedmann, E.I., McKay, C.P., 2006. Hypolithic cyanobacteria, dry
328 limit of photosynthesis, and microbial ecology in the hyperarid Atacama Desert. Microbial
329 Ecology 52, 389-398.
330 Wierzchos, J., DiRuggiero, J., Vitek, P., Artieda, O., Souza-Egipsy, V., Skaloud, P., Tisza, M.,
331 Davila, A.F., Vilchez, C., Garbayo, I., Ascaso, C., 2015. Adaptation strategies of
332 endolithic chlorophototrophs to survive the hyperarid and extreme solar radiation
333 environment of the Atacama Desert. Frontiers in Microbiology 6, 934.
334 Wilhelm, M.B., Davila, A.F., Eigenbrode, J.L., Parenteau, M.N., Jahnke, L.L., Liu, X.,
335 Summons, R.E., Wray, J.J., Stamos, B.N., O'Reilly, S.S., Williams, A., 2017.
336 Xeropreservation of functionalized lipid biomarkers in hyperarid soils in the Atacama
337 Desert. Organic Geochemistry 103, 97-104.
338 Ziolkowski, L.A., Wierzchos, J., Davila, A.F., Slater, G.F., 2013. Radiocarbon evidence of
339 active endolithic microbial communities in the hyperarid core of the Atacama Desert.
340 Astrobiology 13, 607-616.